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FURTHER OBSERVATIONS ON *HIPPONIX ANTIQUATUS* WITH NOTES ON NORTH PACIFIC PULMONATE LIMPETS[1]

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Introduction

The observations on mesogastropod and pulmonate limpets here recorded represent continuation of earlier work on *Hipponix antiquatus* (Linnaeus) and on *Trimusculus (Gadinia) reticulata* (Sowerby) (Yonge, 1953, 1958) carried out in California, while examination of *Siphonaria alternata* Say at Bermuda (Yonge, 1952) forms the basis for the notes on two north Pacific siphonariids. Aeknowledgments for assistance are gratefully made to Dr. L. R. Blinks and Dr. D. P. Abbott of the Hopkins Marine Station, Pacific Grove, where the bulk of the work was done; to Mr. James A. McLean, of Stanford University, who collected specimens of *Williamia vernalis* by diving and provided information about this and other species; to Dr. R. L. Fernald, Acting Director of the Friday Harbor Laboratory, who collected the specimens of *Siphonaria thersites* from San Juan Island which were examined in the Department of Zoology, University of Washington; and to Mr. W. J. Eyerdam of Seattle for shells of this species collected by him in Alaska.

1. From the Hopkins Marine Station, Pacific Grove, and the Department of Zoology, University of Washington.

Hipponix antiquatus (Linnaeus)

Although far from uncommon from mid-tidal levels downward on exposed rocky shores, *H. antiquatus* often demands careful search owing to its habit of living in narrow, often overhung, crevices. Earlier study (Yonge, 1953) had emphasized the very specialized sedentary habit with secretion of a ventral "valve" cemented to the substratum. Surprisingly it is not a ciliary feeder like the related Calyptraeidae and Capulidae, but gropes for food, largely fragments of calcareous algae, by means of the proboscis. In the course of the present observations, animals were seen to extend the proboscis well beyond the margins of the shell and actively to search for and to swallow such fragments. All animals previously examined in 1949, were females and the tentative conclusion was reached that *H. antiquatus* is a protandrous hermaphrodite in which "owing to the sedentary habit and to the rough water in which it lives, cross fertilization may be impossible and it appears more probable that spermatozoa produced during the male phase are stored in the receptaculum for fertilization of eggs produced in the subsequent female phase." Such a condition is known to exist in the bivalve wood borer, *Xylophaga dorsalis* (Purchon, 1941).

Habits. Important additional information about the habitat and numbers of this species was provided by the effects of the great storm which struck the coast of central California on February 16, 1960. Coinciding with spring tides this did extensive damage and granite blocks of great size and weight were displaced on the exposed northwestern side of Point Cabrillo where the Hopkins Marine Station is situated. The floor and roof of often extensive but previously inaccessible crevices into which a hand could not have been inserted, were exposed together with a rich and characteristic fauna of largely attached animals. The more varied fauna, to be mentioned later when discussing *Trimusculus,* covered the roof, i.e., occupied the previous undersurface of the turned boulders. But the uncovered floor (never the roof) was usually thickly covered with either the shells of living *H. antiquatus* or with recent scars. Adjacent animals often touched one another. Thus 45 animals were counted in an area 25 by 20 cm. and 59 animals or recent scars in another area some 15 cm. square. The shells ranged from 8 to 20 mm. in greatest aperture diameter although this is an indifferent criterion of either size or age because the height varies greatly.

Presence of males. Revelation of the large populations within this protected and, clearly for these animals, ideal habitat raised again the question of the presence of males. These, however, could certainly not be mobile, as they are in the Calytraeidae or in *Capulus,* beause all specimens of *H. antiquatus* were cemented. Representative samples were taken from these areas and examination soon revealed the presence of males.

As shown in figure 1, these individuals possess a penis which comes off, as in other Mesogastropoda, at the base of the right cephalic tentacle. What is unusual is the length and bifid end of this organ in *A. antiquatus*. Even when still very wrinkled and clearly capable of much further distension, it may extend beyond the margin of the shell (fig. 1). It may also contract into

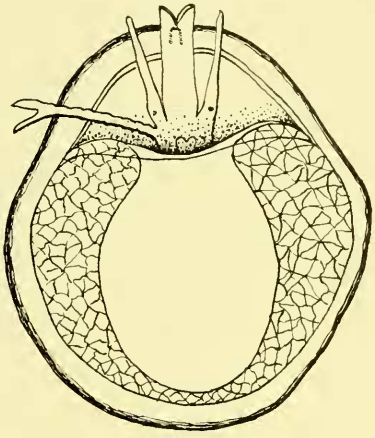

Figure 1. *Hipponix antiquatus*, male, viewed from ventral aspect after removal of under "valve." Note presence of extensile, bifid penis on right side. × 14.

a rounded mass within the mantle cavity. The seminal groove extends along the posterior side of the penis and so along that surface of the posterior terminal bifurcation, opening at the tip of this. The function of the anterior limb must remain conjectural until the process of copulation has been observed which requires examination of colonies of attached individuals. Possibly it attaches to the margin of the shell of an adjacent female while the functional tip of the penis enters the oviduct.

Of 89 animals examined, 13 were males (one with only a rudimentary penis) and 76 females. The former ranged in aperture length from 6.0 to 10.0 mm.; the latter from 7.0 to 20.0 mm. There is thus evidence that the animals are protandric hermaphrodites. Part of the length overlap is certainly due to the extremely variable shape of the shells. The disparity in numbers between the sexes may be due to the time of year: 23 out of the 76 females were carrying egg capsules with young in all stages of development. Fertilization of many animals must therefore have occurred and many former males may have lost the penis in the process of sex change.

Revelation of the presence of these dense colonies of *H. antiquatus* in the protection of deep crannies helps in the understanding of the mode of life of this and allied species. Settlement must take place almost immediately

after hatching when the young crawl vigorously; their behavior being such as to keep them in darkness and on the floor of the rock cleft. The presence of an unusually long penis will enable the attached male to fertilize adjacent females in the same manner that the hermaphrodite acorn barnacles fertilize each other. It is not unusual to find isolated specimens of *H. antiquatus* but it does not seem possible that they can either fertilize in the male phase or be fertilized in the female phase. However, the presence of these dense and well protected colonies will ensure the continuance of the population.

Trimusculus reticulatus (Sowerby)

Further information about the habitat, and also abundance, of this pulmonate limpet of which the mantle cavity and habits have previously been described (Yonge, 1958) was also provided by the effects of the storm on February 16, 1960. What had formed the upper surfaces of these low and extensive crannies were found richly covered with encrusted animals. These included the barnacles, *Tetraclita squamosa rubescens* and *Balanus nubilis,* a variety of serpulids, and, among Mollusca, *Chama pellucida* (which, unlike *Pseudochama exogyra,* does not settle among weeds on more exposed rock faces), *Pododesmus macroschisma,* and *Hinnites multirugosus,* the last two being by no means confined to such an environment. But the most characteristic member of this roof fauna was *T. reticulata.* It is just as confined to the roof of these crevices as *Hipponix* is to the floor. And, like that species, it occurs in compact colonies with shells often in contact. In one area some 30 by 12 cm. there were 51 animals, in another, 22 by 12 cm., 47 were counted. The limpets varied in diameter from 8 to 28 mm.

Internal fertilization is just as essential to these hermaphrodite pulmonates as to mesogastropods such as *Hipponix.* But a gregarious habit might seem less important because *T. reticulata* is certainly mobile, moving actively in aquaria where it crawls up to the water level and above, there respiring in air (Yonge, 1958). Despite this power of movement, the colonies exposed on the upper surfaces of overturned rocks persisted unchanged for certainly six weeks after exposure although this must involve death in the heat of summer. While intertidal species of *Acmaea* so exposed out of their normal environment would quickly have dispersed, behavior in *T. reticulata* is apparently restricted to upward movement (hence their concentration on the roof of crevices) and away from water and, possibly, light. This unnatural exposure on a flat surface in the upper intertidal region provokes no reaction. There is no upper surface on which to move, water seldom reaches them, and there is no gradient of illumination.

Presumably, the young which crawl out of the egg masses (not yet observed) go normally to maintain or swell the existing colony in the particular rock crevice. This specialized habit, resembling—apart from the retention of

mobility—that of *Hipponix,* is in sharp contrast to the less ecologically restricted habit of most Siphonariidae (Yonge, 1958).

Siphonariidae

These highly successful pulmonate limpets are extremely abundant in the Southern Hemisphere especially in the Indian Ocean and the western Pacific. Few species occur in the Northern Hemisphere. Around North America, *Siphonaria alternata* Say and *S. pectinata* Linnaeus occur along southern Atlantic shores, the former extending to Bermuda where it is abundant intertidally on the pitted aeolian limestone (Yonge, 1952). It grips firmly, has a stout shell, and possesses all the adaptations of an intertidal limpet. On the Pacific Coast, *S. thersites* Carpenter ranges from the Aleutian Islands to the Straits of Juan de Fuca, *S. brannani* Stearns from Santa Barbara to Laguna Beach, while the allied *Williamia vernalis* Dall occurs along the entire coast of California with *W. peltoides* Carpenter along the southern half of this, extending into the Gulf of California (Oldroyd, 1927: Keen, 1937).

Two of these species, *S. thersites* and *W. vernalis,* were examined in life and proved of great interest because of the contrast they present to conditions in *S. alternata,* itself probably broadly representative of the great majority of the siphonariids.

Siphonaria thersites Carpenter

The specimens examined were collected by Dr. R. L. Fernald on the rocky shore near Kanaka Bay on the western, more exposed, shore of San Juan Island where they live high on the shore associated with *Fucus.* Compared with *S. alternata* and certainly the great majority of other species of the genus, the thin and asymmetrically coiled shell with the apex near the posterior end is very small (fig. 2). It is flattened and caplike with the characteristic siphonal extension on the right side and appears to be perched on top of the column of the relatively massive foot (fig. 3). The animal cannot be contained within it. The head is small, without tentacles but with minute eyes marginally on the upper surface. The limited overhang of mantle and shell implies that there is effectively no pallial groove. The characteristic siphonariid siphon, with the anus opening on it, projects to the level of the widened shell margin on the right side. The surface of the tall foot is covered with some six rows of white glands which, on mechanical stimulus, produce a very copious densely white and viscid secretion. They also occur on the head and the siphon. These glands occur in all siphonariids examined and are probably repugnatorial, indeed in *A. thersites* they appear to represent the sole means of defense.

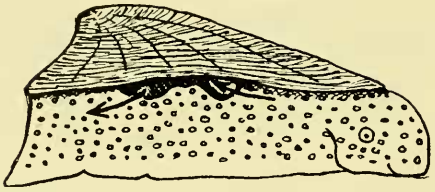

Figure 2. *Siphonaria thersites*, viewed from right side, showing siphon with arrows indicating inhalant and exhalant currents, also glands on sides of foot and on head. × 14.

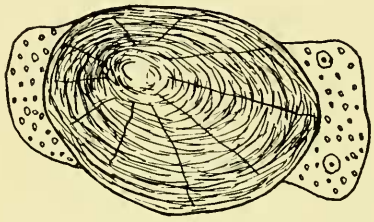

Figure 3. *Siphonaria thersites*, viewed from above when crawling, showing extension of head in front and foot behind the small asymmetrical shell. × 14.

Outside the mantle cavity the surface is unciliated, precisely as in *S. alternata*. A slow current enters the mantle cavity by the anterior, inhalant, opening and leaves by the exhalant opening on the posterior side of the siphon. Within the cavity there is precisely the same arrangement of organs as described in *S. alternata* (Yonge, 1952). The filaments of the secondary gill hang down from the roof but the respiratory current is largely produced by dense cilia on an underlying ridge on the floor of the cavity. These secondarily acquired but undoubtedly highly efficient respiratory organs possibly represent a major factor in the success of the Siphonariidae. The much more restricted *Trimusculus* has no such gills (Yonge, 1958).

The habitats of *S. thersites* are most interesting. Alike at San Juan Island and in Alaska it occurs on *Fucus*. It feeds on this, excavating rounded depressions and discharging long faecal threads of fucoid materials from the anus as it does so. The animal is active for a limpet; it crawls quickly along *Fucus* or on a glass surface groping with the broad, rather suckerlike head. The general appearance is shown in figure 3. There is a tendency to move up the sides of an aquarium. It appears that this species occurs in cracks in rocks during the summer so achieving protection from high insolation. Probably it emerges to feed on *Fucus* by night. The unusual reduction of the shell and accompanying greater mobility may therefore be associated with the mode of life, the animal feeding on *Fucus* high on relatively exposed shores where protection is needed both against the heat of the sun in the

summer and also from storms. It may even hibernate under such conditions at the northern end of its range.

Siphonaria thersites may therefore be regarded as a siphonariid of specialized and restricted habitat. This could account for its far northern distribution.

Williamia vernalis Dall

The obvious difference between the shell in this genus and in the closely related *Siphonaria* is the absence in the former of a siphonal projection. The shell in *W. vernalis* is smooth and perfectly symmetrical with a backward pointing apex some one-third of the distance from the posterior end. The shell is reddish brown with lighter colored rays radiating from the apex (see Oldroyd, 1927, for full description).

The appearance of the animal when viewed ventrally is shown in figure 4. Although Mr. McLean states that fully grown animals are blue, the young specimens examined, the largest with a shell aperture 5.5 mm. long by 4.0 mm. wide, were all bright red. This pigmentation occurs on the sides of the foot, on the top of the head, and on the mantle although there it forms radiating bands alternating with lighter areas, six on each side, in which the white glandular patches are conspicuous. Equally numerous on all surfaces, they

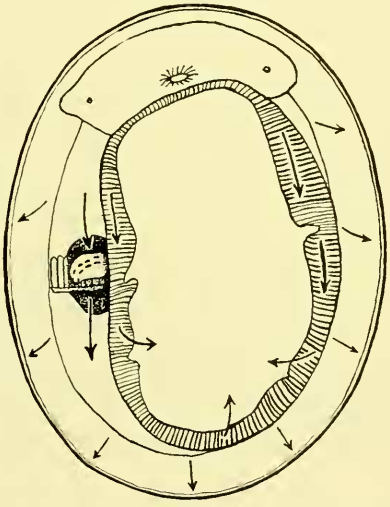

Figure 4. *Williamia vernalis*, viewed from ventral aspect showing head with small mouth, foot (sides shaded) and large pallial opening, with siphon (bearing anus) on right side. Marginal pallial gills shown. Arrows indicate inhalant and exhalant currents also cleansing currents in pallial grooves (rejection via posterior surface of foot). × 24.

are obscured in the pigmented areas. The mantle is more extensive than in *S. thersites* (although not more so than in *S. alternata*), the shell which it secretes being pulled down completely over the animal. Indeed the head barely projects beyond this when moving. The wide and deep pallial grooves so formed differ from those of the other two species in being ciliated. As indicated by the arrows in figure 4, particles are carried rapidly backward within the groove and along the sides of the foot and then rejected by way of the sole of this posteriorly. Peripherally there is an outward movement of particles along the mantle margin.

The head has the typical siphonariid appearance, flattened, without tentacles, and with a pair of minute eyes. The pallial opening is wide and much internal structure can be seen without dissection; the most marginal of the pallial gills can be seen from the ventral view (fig. 4). The width of the inhalant and exhalant openings through which powerful currents pass may explain the absence of a siphonal extension to the shell in this genus. The disposition and mode of functioning of the pallial organs are the same as in *S. alternata*.

The habits and habitat of *W. vernalis* are in interesting contrast to those of *S. alternata* and *S. thersites*. The first of these is midtidal (Yonge, 1952), the second, as reported above, is a specialized inhabitant of the upper shore. *Williamia vernalis*, on the other hand, occurs very low on the shore, to be collected only at low spring tides and, more suitably, by diving in the shallow sublittoral. It occurs there on the shells of *Tegula brunnea*, sometimes dead and inhabited by hermit crabs, or on those of *Astrea gibberosa*, as well as on rocks, but probably always associated with the presence of red coralline algae on which it appears to feed. In movement the broad head lobes move actively from side to side as the animal explores the surface over which the radula scrapes. From his observations while collecting, Mr. McLean considers that *W. vernalis* requires a protected environment. The delicate shell would indicate this but most of all the presence of powerful cleansing currents in the pallial grooves. This provides evidence that this limpet lives in regions where water movements are too weak to ensure cleansing, in contrast to conditions in *Lottia gigantea* (Abbott, 1956) and in the majority of local intertidal species of *Acmaea* (personal observations) where cleansing is brought about by water movements. And this is also true of the two species of *Siphonaria*.

Summary

Overturning of major boulders in the upper tidal region on Point Cabrillo, Pacific Grove, by a major storm on February 16, 1960, revealed dense colonies of *Hipponix antiquatus* on the floor of previously inaccessible crevices. The presence of nonmotile males having an unusually extensile and

bifid penis was established but all the larger animals were female, indicating protandry. Maintenance of this attached species is probably ensured by the existence of these dense, well protected colonies.

Equally dense colonies of the pulmonate limpet *Trimusculus reticulatus* occurred on the roof of these crevices. This concentration appears to be the result of behavior and ensures cross-fertilization and protection from desiccation.

Siphonaris thersites lives associated with *Fucus* on the upper shore in the north Pacific. Mobility due to reduction of the shell enables it to find protection from insolation within cracks in the rocks.

Williamia vernalis is an inhabitant of the low intertidal and shallow sublittoral. Absence of the siphonal extension of the shell in this genus may be due to the wider opening into the pallial cavity. The presence of cleansing cilia in the pallial grooves indicates life in sheltered areas of still water.

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